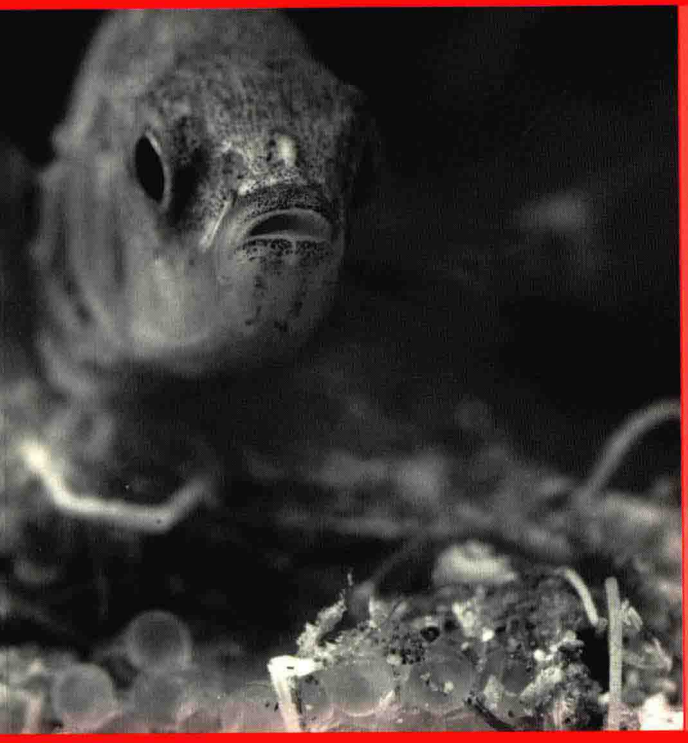
Ecological Speciation

Patrik Nosil



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Ecological Speciation

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Preface

I undertook the writing of this book during a yearlong stay at the Institute for Advanced Study, *Wissenschaftskolleg*, in Berlin, Germany. At that point in time, I had been involved in speciation research for about a decade. However, upon commencing the writing of the book, it came clear how little I knew. Thus, writing this book was a true learning experience, and one that was made possible only by the freedom from other academic responsibilities that was provided by the *Wissenschaftskolleg*. For this, I am greatly indebted to the *Wissenschaftskolleg* and to Axel Meyer for inviting me to participate in a working group there. I thank Axel and the other two members of that group, Jim Mallet and Jeff Feder, as well as fellow Robert Trivers for ongoing scientific discussions concerning speciation. I thank Hélène Collin for many discussions during the writing of this book, and for enduring many days and nights in Berlin where all I did was work on the book.

Although I commenced the task of writing that year in Berlin, it took three years to complete the project. Numerous people are to be thanked. In particular, I am most indebted to my mentors over the years. In particular, I thank those involved in my entry into research in evolutionary biology, including Tom Reimchen, Bernie Crespi, Cristina Sandoval, Arne Mooers, Felix Breden, and Dolph Schluter. Tom has provided an endless source of inspiration and motivation. At times in our scientific careers we are lucky enough to meet exceptional people, those with truly thoughtful and unique perspectives. These are the people that when they open their mouths, we know we should listen carefully to what they say, even if ultimately we might disagree. Tom has been that person for me. Others, such as Dolph, have played similar roles. Dolph's work strongly influenced me, and his support and insight over the years cannot be overstated, and is much appreciated. More recently, I had the fortune to engage in a fun and fruitful collaboration with Jeff Feder. Discussions with him influenced me in positive and creative ways. I thank my mentors for their ongoing support, as well as their constructive criticism.

For comments on drafts of specific chapters of the book, I thank Scott Egan, Matt Wilkins, Joey Hubbard, Rudy Riesch, Kei Matsubayashi, Issei Ohshima, Justin Meyer, Sergey Gavrilets, David Lowry, Daniel Ortiz-Barrientos, Rowan Barrett, Scott Pavey, Yael Kisel, Fred Guillaume, and Jim Mallet. My doctoral students, Tim Farkas and Aaron Comeault read a draft from cover to cover, providing much

constructive criticism along the way. For this, I am indebted. Dolph Schluter and Ole Seehausen provided numerous useful comments on a complete draft. The book benefited from discussion with members of a graduate course on speciation, including Matt Wilkins, Joey Hubbard, Loren Sackett, Se Jin Song, Sharon Aigler, Rebecca Povilus, Brent Hawkins, Timothy Farkas, Christine Avena, Amanda Wills, Robert Jadin, and Bader AlHajeri. Finally, I thank numerous other co-authors and colleagues with whom I have worked on and discussed speciation with, including Hélène Collin, Maria Servedio, Daniel Funk, Michael Kopp, Sander Van Doorn, Rebecca Safran, Samuel Flaxman, Axel Meyer, Scott Egan, Zach Gompert, Tom Parchman, Alex Buerkle, Daniel Ortiz-Barrientos, Sean Rogers, Christine Parent, Steve Springer, Jeff Joy, Rutger Vos, Andrew Hendry, John Endler, Michael Turelli, Trevor Price, Jenny Boughman, Daniel Bolnick, Juan Galindo, Daniel Duran, Gabriel Perron and Howard Rundle. I extend my apologies to anyone forgotten, and am very grateful for the many friends within the scientific community that I have had the pleasure of interacting with.

I also thank my parents and sister for their lifelong support of whatever curiosities engaged me at the time. I thank my editors at Oxford University Press, Helen Eaton and Ian Sherman, for their advice and encouragement. Finally, I note that although this book clearly could not have come to fruition without the support and intellect of numerous colleagues, any errors contained within are my responsibility alone.

Introduction

Adaptation to different ecological environments, via divergent natural selection, can generate phenotypic and genetic differences between populations. In turn, these changes might create new species. The general aim of this book is to synthesize the theoretical and empirical literature on the formation of new species due to divergent selection. This process of "ecological speciation" has seen a large body of particularly focused research in the last 15–20 years, and thus it is an excellent time for a review and synthesis. A particularly important goal will be the integration of the ecological and genetic literature. Both ecological studies of the sources of natural selection and genetic studies of the genes and genomic regions affected by divergent selection have accumulated, but they have yet to be strongly integrated. Such integration will hopefully shed new insight into the speciation process.

This book necessarily focuses to a large extent on the predictions and tests of ecological speciation, and on reviewing its three main components: (1) a source of divergent natural selection; (2) a form of reproductive isolation; and (3) a genetic mechanism to link divergent selection to reproductive isolation. However, a critical aspect that sets the book apart from past treatments of speciation will be the inclusion and further development of some recent concepts that particularly apply to ecological speciation. For example, the concept that natural selection against immigrants into foreign environments (i.e., "immigrant inviability") can reduce interbreeding between populations, and thus act as a barrier to genetic exchange, unifies the study of divergent adaptation and speciation (Nosil et al. 2005). The concept of "genomic islands of divergence" is a useful metaphor for considering how the diversifying effects of selection spread throughout the genome during the speciation process (Turner et al. 2005). Similarly, "isolation-by-adaptation" describes how selection affects patterns of genetic divergence, even potentially for neutral genes unlinked to those under divergent selection, by reducing gene flow to the extent that genetic drift can occur at all loci (Nosil et al. 2008). These concepts will all be explored in depth in this book. Finally, a central theme of the book, one that is receiving much current attention in the literature, will be the often-continuous nature of divergence during the speciation process (Mallet et al. 2007, Berner et al. 2009, Peccoud et al. 2009).

The above-mentioned concepts, and the explicit focus on the mechanism of speciation via divergent selection, set this book apart from excellent past books on speciation. For example, Mayr's (1942, 1963) treatments of speciation predate the DNA sequence era. Schluter (2000b) devoted a chapter explicitly to ecological speciation but focused on adaptive radiation more broadly. Coyne and Orr (2004) covered overall patterns of speciation and thoroughly reviewed the genetic basis of reproductive isolation, but the breadth of their book necessarily precluded an exhaustive treatment of ecological speciation. The edited volume by Dieckmann et al. (2004) examined "adaptive speciation" due to frequency-dependent disruptive selection. However, adaptive speciation is a special case of ecological speciation because adaptive speciation, unlike ecological speciation, is restricted to cases where frequency-dependent disruptive selection in sympatry or parapatry drives speciation. Thus, unlike this book, Dieckmann et al. (2004) did not treat cases of allopatric divergence or cases in which divergent selection was not frequency-dependent. Price (2007) covered speciation, but focused on birds. Other books on speciation were edited volumes, and thus contained many useful different views and topics, but did not focus systematically on ecological speciation (Otte and Endler 1989, Howard and Berlocher 1998, Butlin et al. 2009). This book aims to build upon and expand the treatments of ecological speciation that rest within each of these previous books, as well as to provide an empirical counterpart to theoretical treatments of ecological speciation in Endler (1977) and Gavrilets (2004).

This book covers extensive literature, but owing to the rapidly growing nature of the field, not all aspects can be exhaustively covered. In numerous sections, I provide comprehensive and relatively exhaustive reviews, often in the form of tables. However, in many other points of the text I draw upon key examples that illustrate the point at hand. The book itself is organized into three main sections. The first section deals with clarifying what ecological speciation is, its predictions, and how to test for it (chapters 1 and 2). This sets up the second part of the book, which reviews the three components of ecological speciation. It is useful to devote a separate chapter to each component because each can be studied, to a certain extent, independently from the others. This approach also helps highlight areas that have received less attention, and is warranted because data within any given system usually exists for only one or two components. Chapter 3 thus reviews the sources of divergent selection: namely, environmental differences, interactions between populations, and ecologically dependent sexual selection. Chapter 4 reviews the forms of reproductive isolation that occur during ecological speciation, including their relative contributions to total reproductive isolation and the temporal order in which they evolve. Chapter 5 considers the genetic mechanisms that link selection to reproductive isolation, as well as the individual genetic bases of adaptation and reproductive isolation during ecological speciation.

The third and final section of the book deals with other outstanding topics in the study of ecological speciation. Chapter 6 considers the geography of ecological speciation, including how geography affects the sources of selection, how gene flow might promote or constrain divergence, and the possibility of multiple geographic

modes of divergence during any single instance of speciation. Chapter 7 reviews the genomics of ecological speciation, focusing on how selection generates variation among genomic regions in their levels of genetic differentiation between populations. The role of gene expression in speciation is also considered. Chapter 8 focuses on variability in how far the often-continuous process of speciation proceeds. This chapter considers whether partial reproductive isolation is often a stable outcome (i.e., an equilibrium) and offers hypotheses for variation in how far ecological speciation proceeds. The final chapter of the book focuses on particularly pressing questions that remain.

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Abbreviations

AFLP	amplified fragment length polymorphism
CD	character displacement
ECD	ecological character displacement
ERG	ecology, reproductive isolation, genetic distance
eQTL	expression quantitative trait locus
IBA	isolation-by-adaptation
IBD	isolation-by-distance
IM	isolation with migration
mtDNA	mitochondrial DNA
NIL	near-isogenic line
pQTL	phenotypic quantitative trait locus
QTL	quantitative trait locus
RCD	reproduction character displacement
RI	reproductive isolation
SNP	single nucleotide polymorphism

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